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Converting low dose radiation to redox signaling

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Abbreviations: PGA, polygalacturonic acid; $^{\bullet}OH$, hydroxyl radical; $^{\bullet}O_2^-$, superoxide radical anion; H_2O_2, hydrogen peroxide; SOD, superoxide dismutase

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In contrast to the damaging effects of high doses, low dose radiation (UV, gamma) has been reported to provoke constructive changes in plants. However, the mechanisms by which plants recognize and respond to low dose radiation are not understood. We have shown recently that polygalacturonic acid, cell wall polysaccharide, converts the highly reactive product of radiation - hydroxyl radical into superoxide which may be further dismutated to hydrogen peroxide. Superoxide has been proposed to act as a signaling molecule, while hydrogen peroxide is known to be the key species in redox signaling cascades which are involved in the regulation of various physiological processes. Hence we propose that polygalacturonic acid may operate as radiation-signaling convertor. The outlined principles of radiation-sensing could also be valid for mammalian cells, with some other molecules mediating the conversion.

In the recently published paper,[1] we have substantiated previous assertions that the components of cell wall - galacturonic acid polymers (polygalacturonic acid (PGA), oligogalacturonic acid, and pectic fragments) are capable of transforming hydroxyl radical ($^{\bullet}OH$) into superoxide radical anion ($^{\bullet}O_2^-$).[2] The mechanism involves the reaction of $^{\bullet}OH$ with carboxyl groups in galacturonic acid moieties, which results in the production of carbon-centered radicals - carbon dioxide radical and pectin C(5) radical.[1-3] These radicals further react with molecular oxygen having $^{\bullet}O_2^-$ as an end product. The step that is enabled by PGA is huge. Namely, PGA 'takes' the most reactive species in the living systems - $^{\bullet}OH$, which shows half-life time of ~10^{-9} s and has exclusively damaging effects, and turns it into $^{\bullet}O_2^-$, which is approximately three orders of magnitude less reactive and may act as a signaling molecule (**Fig. 1**).[4,5] In our experimental setup, the source of $^{\bullet}OH$ was UV-provoked homolysis of hydrogen peroxide (H_2O_2).[1] UV is known to activate various signaling pathways in plants and to affect plant biochemistry, physiology, and gene expression. This may lead to altered biomass allocation, timing of plant development, branching, leaf and canopy architecture and other processes.[1] Our results clearly add up to the understanding of the mechanisms by which UV irradiation sets off constructive changes, but the implications go far beyond, as some other types of environmental radiation, such as gamma, possess enough energy to produce $^{\bullet}OH$ from water. In this case, signaling cascades may be also initiated by H_2O_2 which is produced from $^{\bullet}O_2^-$ by superoxide dismutases (SOD) (**Fig. 1**).

Pertinent to this, the increased level of H_2O_2 in plants exposed to gamma radiation is well documented, the highest concentrations being observed in leaves,[6] while SOD activity has been closely related to the adaptive responses provoked by low dose radiation.[7,8] Hydrogen peroxide is the key species in redox signaling showing the ability to modulate different biological processes by activating/inhibiting gene transcription and enzyme activity.[5,9] Even more, at concentrations in the high physiological range, H_2O_2 induces more permanent, modifying changes, adaptations, increasing the resistance of biological systems to the same stimulus (hormesis) or other stressors (cross-adaptation).[5,9]

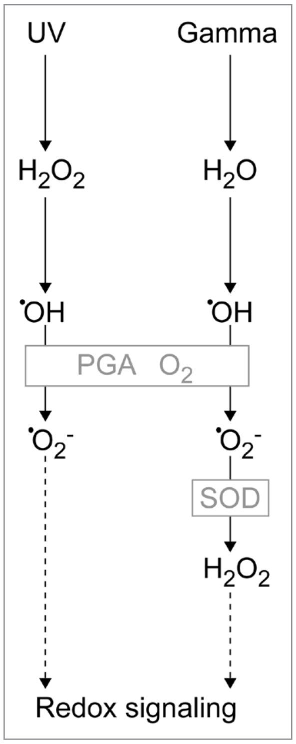

Figure 1. The principles of low dose radiation-redox signaling conversion conducted by PGA in plants.

Ionizing radiation is recognized to create perturbations in the homeostatic equilibrium (metabolism) as well as reversible or irreversible damage (structural changes) which may be detected at the molecular level by sensitive physical, chemical and biological (omics) methods. However, some low dose radiation effects in plants are not in accordance with the linear no-threshold (LNT) dose response model. It has been reported that low dose gamma radiation provokes in plants: various physiological changes on the cellular level,[6] promoted expression of specific genes, e.g., those for antioxidative defense enzymes,[10-12] hormesis,[13] cross-adaptation to UV-B irradiation, high-intensity light, and drought stress,[11,14] increased biomass yield, plant vigor and growth, and grain yield,[11,15-17] fruit ripening,[18] enhancements of embryogenesis,[19] and additional trichome formation.[8] The link between PGA and low dose gamma radiation-activated redox signaling cascades is implicated by the observation that the radiation induces drastic inhibition of PGA-decomposing enzyme polygalacturonase and the upregulation of pectin methylesterase,[18] thus preserving PGA structure and at the same time making carboxyl groups on pectin available for conducting $^{\bullet}OH \rightarrow {}^{\bullet}O_2^-$ conversion. Even more, it has been shown that low dose gamma radiation-provoked trichome formation in Arabidopsis was prevented by the supplementation of antioxidants, and it has been proposed that the effects are mediated by reactive oxygen species generated by water radiolysis.[8]

The transformation of the primary product of H_2O_2 UV-lysis and water radiolysis - $^{\bullet}OH$ to signaling species - $^{\bullet}O_2^-$ and H_2O_2 may explain how plants recognize and respond to radiation. However, low doses of radiation induce protective effects based on responses that have been tightly conserved throughout evolution, suggesting that they are critical to life.[13] Hence, analogous mechanisms of radiation to redox signaling conversion may be present in other organisms. It has been postulated that manganese SOD, a fundamental mitochondrial redox enzyme in mammalian cells, plays a key role in the low dose ionizing radiation-induced adaptive response.[7] It can be speculated that $^{\bullet}OH$ transformation into $^{\bullet}O_2^-$ may be the inducer of SOD-related response not only in the plants but also in mammalian cells indicating possible presence of some radiation-signaling convertor with the same ability as PGA also in mammalian cells.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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